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A New Poison Frog (*Dendrobates*) from Andean Colombia, with Notes on a Lowland Relative

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ABSTRACT

Dendrobates andinus, new species, is a small arboreal frog from wet montane forest (1700–2020 m elev.) on the Pacific versant of the Andes in extreme southwestern Colombia. Although its color pattern—yellowish dorsolateral stripes on a black or dark brown body—is reminiscent of two other Colombian species (*D. truncatus* and *Phyllobates aurotaenia*), *D. andinus* is not closely related to them. *Dendrobates andinus* is tentatively placed in the *pictus* species group, in which its closest relative seems to be *D. erythromos* Vigle and Miyata, from lowland rain forest (170 m elev.) on the Pacific side of Ecuador. The recently described “*Phyllobates*” *azureiventris* Kneller and Henle, from Amazonian Peru, incidentally, is also transferred to the *pictus* group of *Dendrobates*.

Natural history data for *Dendrobates andinus* include observations on courtship behavior and cephalic amplexus; individuals are most frequently associated with water-filled bromeliads, where clutches of three or four eggs are laid. Sound spectrograms and waveforms of the advertisement call of *Dendrobates erythromos* are provided for future comparison when recordings become available for *D. andinus*, whose call was perceived in the field as a series of well-spaced “creek” notes. The call of *erythromos* is termed a *retarded chirp call* and is briefly compared with the characteristic chirp call of the *histrionicus* species group of *Dendrobates*.

RESUMEN

Dendrobates andinus, especie nueva, es una rana arbórea pequeña que se encuentra en el bosque húmedo montano (altitud 1700–2020 m) de la vertiente Pacífica de los Andes en el extremo suroeste

de Colombia. El patrón de coloración de esta especie consiste en bandas dorso-laterales amarillentas sobre un fondo negro o castaño oscuro, asemejándose así al de *D. truncatus* y *Phyllobates*

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aurotaenia, ninguna de las cuáles se relaciona cercanamente con la especie que se describe. *D. andinus* se coloca tentativamente en el grupo de especies *pictus*, el pariente más cercano del cual es *Dendrobates erythromos* Vigle y Miyata, que se encuentra en el bosque húmedo de tierras bajas (altitud 170 m) en la zona Pacífica de Ecuador. "*Phyllobates*" *azureiventris* Kneller y Henle, recientemente descrita de Amazonas en Perú, incidentalmente se transfiere también al grupo *pictus* de *Dendrobates*.

Observaciones de la historia natural de *Dendrobates andinus* incluyen datos sobre compor-

tamiento de apareo y amplexus cefálico. Los individuos se encuentran muy frecuentemente dentro de bromelias cargadas de agua, donde ponen tres o cuatro huevos por postura. Espectrogramas y las formas de las ondas sonoras del canto de *D. erythromos* son incluidas para una futura comparación cuando se obtengan grabaciones de *D. andinus*, cuyo canto fué percibido como una serie de notas "criiik" bien interespaciadas. El canto de *D. erythromos* se llama un canto de chirrido retardado y se lo compara brevemente con el canto de chirrido característico de las especies del grupo *histrionicus* del género *Dendrobates*.

INTRODUCTION

Gaudily colored diurnal frogs of the genera *Dendrobates* and *Phyllobates* are conspicuous elements of some Neotropical forests. Such genera might be expected to be well known taxonomically. But many species have such small geographic ranges, and may be so secretive (brilliantly colored or not), that the extent of their diversity is only recently becoming appreciated. Almost half of the nearly 50 species currently assigned to *Dendrobates* have been named since 1970, and the senior author is aware of an additional 10 or 11 species still to be described, with others doubtless remaining to be discovered.

The purpose of this paper is to describe one of several unnamed *Dendrobates* occurring in Colombia, and to comment on its natural history and relationships. This frog was noticed first by Mr. Guillermo Cantillo, who pointed it out to the junior author during her work in 1986 at La Planada Nature Reserve in the Andes of extreme southwestern Colombia. The new frog shows a pronounced similarity in coloration with two other Colombian dendrobatids, which, however, are judged not closely related to it (fig. 1).

ACKNOWLEDGMENTS: Field studies by Burrowes were supported by a grant from the George D. Harris Foundation, Washington, D.C. Logistic support at La Planada was provided by the Fundación para Educación Superior (FES), Cali, Colombia. For first calling attention to the new frog, and for other courtesies, we are particularly grateful to Guillermo Cantillo, Superintendent of the Reserva Natural La Planada.

For lending specimens and issuance of export permits, we thank José Vicente Rodri-

guez, INDERENA, Bogotá, Colombia. We are pleased to acknowledge Norma M. Feinberg for preparing radiographs, and John Daly, William E. Duellman, Linda S. Ford, and Linda Trueb for reviewing the manuscript.

ABBREVIATIONS: Collection abbreviations used in this paper are:

AMNH	American Museum of Natural History, New York
IND-AN	Amphibian collection of Instituto Nacional de los Recursos Naturales Renovables y del Ambiente (INDERENA), Bogotá
LP	Reserva Natural La Planada, Pasto, Colombia

Dendrobates andinus, new species

Figures 1A, 2B, 3–5

HOLOTYPE: IND-AN 1556 (field no. PAB 646), an adult female obtained by Patricia A. Burrowes on June 9, 1986, in montane forest at 1780 m elev., in the Reserva Natural La Planada (approx. 1°10'N, 78°00'W), Municipio de Ricaurte, Department of Nariño, Colombia. See map (fig. 6).

PARATYPES: IND-AN 1538, 1539, 1555, same locality as the holotype, collected by P. A. Burrowes in May 1986.

OTHER SPECIMENS: Five additional specimens (LP 432, 528, 536, 552, 820) are housed at the La Planada Reserve, where they were examined by Burrowes. These unsexed specimens, 15.3–22.4 mm in snout-to-vent length (SVL), are not included in the formal description below; two individuals less than 17 mm SVL are probably juveniles.

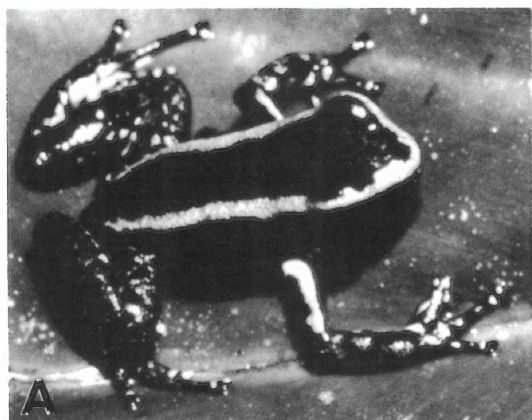


Fig. 1. Three Colombian poison frogs with similar patterns of yellow dorsolateral stripes on a black ground (not to same scale): A. *Dendrobates andinus*, new species. Unpreserved speci-

ETYMOLOGY: The name is a New Latin adjective pertaining to the Andes Mountains.

DEFINITION AND DIAGNOSIS: A small to medium-size dendrobatid having an adult snout-to-vent length of about 19–22 mm. Dorsal surfaces overall dark brown or black, with a pair of yellowish dorsolateral stripes on body and bluish green spots or speckling on limbs; no lateral stripe in groin; ventral surfaces black under throat, variably mottled dark brown and bluish green to yellow on belly and undersides of thighs; an elongated bright yellow marking on the proximoventral surface of the shank (calf spot). Teeth present on maxillary arch. Appressed first finger slightly shorter than second; discs on all fingers moderately expanded; third finger disc of adults about 1.6 times wider than finger.

Dendrobates andinus most closely resembles two other Colombian dendrobatids—*Phyllobates aurotaenia* and *Dendrobates truncatus*—in having a black body with yellowish stripes that are completely dorsolateral (i.e., not descending to the groin posteriorly). Overall pattern resemblance is closest in *P. aurotaenia* (fig. 1B), which is readily distinguished from *D. andinus* in lacking a pale calf spot and in having the appressed first finger decidedly longer than the second (fig. 2). *Dendrobates truncatus* (fig. 1C) is distinguished by pale wavy lines on the limbs and venter, lack of a pale calf spot, relatively larger finger discs (fig. 2), and absence of teeth.

Dendrobates andinus is morphologically similar and probably closely related to *D. erythromos* (figs. 10, 11) from the Pacific lowlands of Ecuador. This slightly larger species is readily distinguished from *andinus* by presence of dark cross-banding on the hind limbs (pale spotted in *andinus*) and bronzy brown dorsolateral stripes that are poorly defined in life and especially vague in preservative (stripes in *andinus* yellowish in life and remaining well defined in preservative). See Systematics section for other comparisons.

←

men from La Planada (type locality), 1780 m, Depto. Nariño. B. *Phyllobates aurotaenia*, AMNH 87145, Quebrada Vicordó, 100 m, Río San Juan, Depto. Chocó. C. *Dendrobates truncatus*, AMNH 85229, Río Gualí near Mariquita, 530 m, Depto. Tolima.

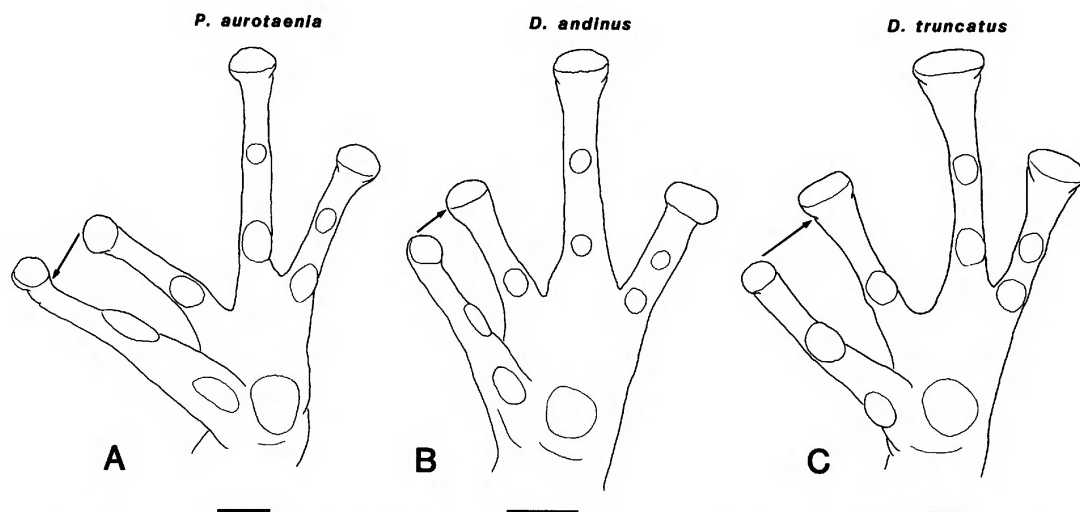


Fig. 2. Palmar view of left hands of three similarly colored dendrobatids (see fig. 1). All adult males; scale lines = 1 mm. Arrows between first two fingers indicate position of the shorter digit when the two are appressed (usually done by pressing *both* fingers together between points of forceps). A. *Phylllobates aurotaenia*, AMNH 85239, $\times 6.75$. B. *Dendrobates andinus*, IND-AN 1555, $\times 9.1$. C. *Dendrobates truncatus*, AMNH 85326, $\times 7.25$.

TABLE 1
Measurements (in mm) for the Type Series of *Dendrobates andinus*, new species

Character	IND-AN 1538 adult ♀	IND-AN 1539 adult ♂	IND-AN 1555 adult ♂	IND-AN 1556 adult ♀
Snout-vent length	20.7	20.1	19.5	21.5
Tibia length ^a	10.8	10.4	9.7	11.0
Greatest body width	7.1	7.8	6.2	9.1
Head width between angles of jaws	7.6	7.0	6.7	7.5
Head width between outer edges of upper eyelids	6.9	6.7	6.3	7.1
Width of interorbital area	2.6	2.7	2.4	2.5
Head length (sagittal) tip snout to angle of jaw	5.6	5.5	5.0	5.7
Tip of snout to center of naris (sagittal)	0.4	0.5	0.4	0.4
Center naris to anterior edge of eye	1.8	1.6	1.7	1.8
Distance between centers of nares	3.1	3.1	2.8	3.1
Eye length, anterior to posterior edge	3.0	3.0	2.6	3.1
Horizontal diameter of tympanum ^b	1.5	1.4	1.2	1.5
Corner of mouth to lower edge of tympanic ring	0.5	0.3	0.7	0.5
Hand length ^c	6.3	6.0	5.6	6.5
Width of 3rd finger disc	0.8	— ^d	0.8	0.8
Width of 3rd finger below disc ^e	0.5	—	0.5	0.5
Width of 3rd toe disc	0.9	0.9	0.8	0.9
Width of 3rd toe below disc ^e	0.5	0.5	0.4	0.5
Width of 4th toe disc	0.9	0.8	0.8	0.8
Width of 4th toe below disc ^e	0.5	0.5	0.5	0.5

^a Tibia measured between heel and outer surface of flexed knee.

^b An approximate measurement (tympanum concealed dorsally and posterodorsally).

^c Hand length measured from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger.

^d Right hand aberrantly shaped; left hand with damaged 3rd toe disc.

^e Digit width measured near distal end of penultimate phalanx.

DESCRIPTION OF TYPE SERIES

Two adult males are 19.5 and 20.1 mm SVL, each with paired vocal slits and a shallow, subgular vocal sac. Two females are 20.7 and 21.5 mm SVL; the smaller of these is adult as shown by large convoluted oviducts and active ovaries in which the largest ova ≥ 0.5 mm, and the larger specimen (the undissected holotype) is judged sexually mature because of its size. See table 1 for comparative measurements.

EXTERNAL MORPHOLOGY: Dorsal and ventral skin smooth to barely granular in preservative. Head width between outer edges of upper eyelids less than width between jaw articulations. Head narrower, or a little wider, than body width. Head width between angles of jaws 34.4–36.7 percent of SVL. Snout sloping, rounded in profile, weakly pointed to truncate in dorsal or ventral aspect. Nares situated near tip of snout and directed posterolaterally; nares visible from front and from below; not (or barely) visible from above. Canthus rostralis rounded; loreal region flat, inclined slightly outward to lip. Interorbital distance wider than upper eyelid. Eye longer than snout length; distance from center of naris to eye 53–65 percent of eye length. Tympanum vertically oval, concealed both dorsally and posterodorsally, smaller than eye.

Hand (fig. 3) moderately large, its length (proximal edge of metacarpal tubercle to tip of longest finger) 28.7–30.4 percent of SVL, 82.9–86.7 percent of head width (at jaw articulations). Relative length of *appressed* fingers $3 > 4 > 2 > 1$; appressed first finger little shorter than second, its tip reaching or overlapping disc of second (fig. 2B). Discs moderately expanded on fingers, including the first; third finger disc in one male and two females 1.6 times wider than distal end of adjacent phalanx. A large circular outer metacarpal tubercle on median base of palm, an elliptical inner metacarpal tubercle on base of first finger, and one or two subarticular tubercles on fingers (one each on fingers 1, 2; two each on fingers 3, 4); all tubercles low, with rounded surfaces.

Hind limbs relatively long, with heel of appressed limb reaching between eye and snout; tibia 49.7–52.2 percent of SVL. Rel-

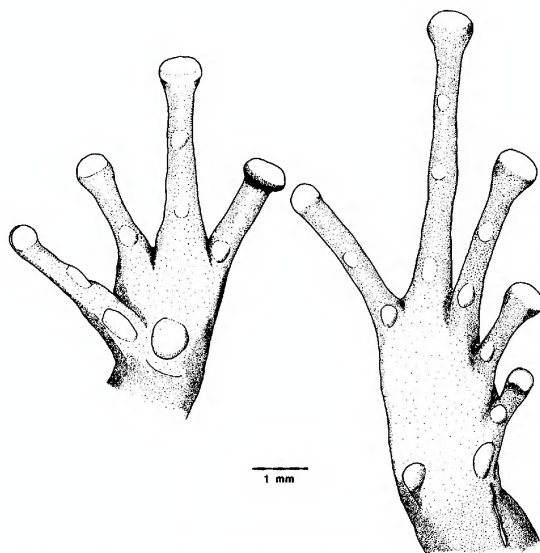


Fig. 3. Left hand and right foot of *Dendrobates andinus*, new species. IND-AN 1555, adult male paratopotype, $\times 7$.

ative lengths of appressed toes $4 > 3 > 5 > 2 > 1$; first toe reaching subarticular tubercle of second. First toe with slightly expanded disc, other toes with moderately expanded discs about as large as or slightly larger than finger discs (fig. 3). One to three nonprotuberant, sometimes indistinct, subarticular tubercles (one each on toes 1, 2; two each on 3 and 5; three on 4); no basal webbing. A slightly protuberant outer metatarsal tubercle, and a low, nonprotuberant inner metatarsal tubercle. A narrow, sharply defined tarsal ridge present on inner side of distal third of tarsus (fig. 3); no discrete tubercle at proximal end of tarsal ridge.

COLOR PATTERN: In life (fig. 1A), the head and body are shiny dark brown to black with a pair of greenish yellow dorsolateral stripes, which are continuous around the top of the snout and extend posteriorly along the canthi rostrali and over the eyelids, to terminate near the vent above the thighs. The hind limbs are shiny dark brown dorsally, with small bluish green spots on limbs and feet. Arms brown dorsally, with or without an elongated yellow marking on anteroproximal part of upper arm and with small bluish green spots on forearms and hands.

Throat and chest dark brown to black. An-

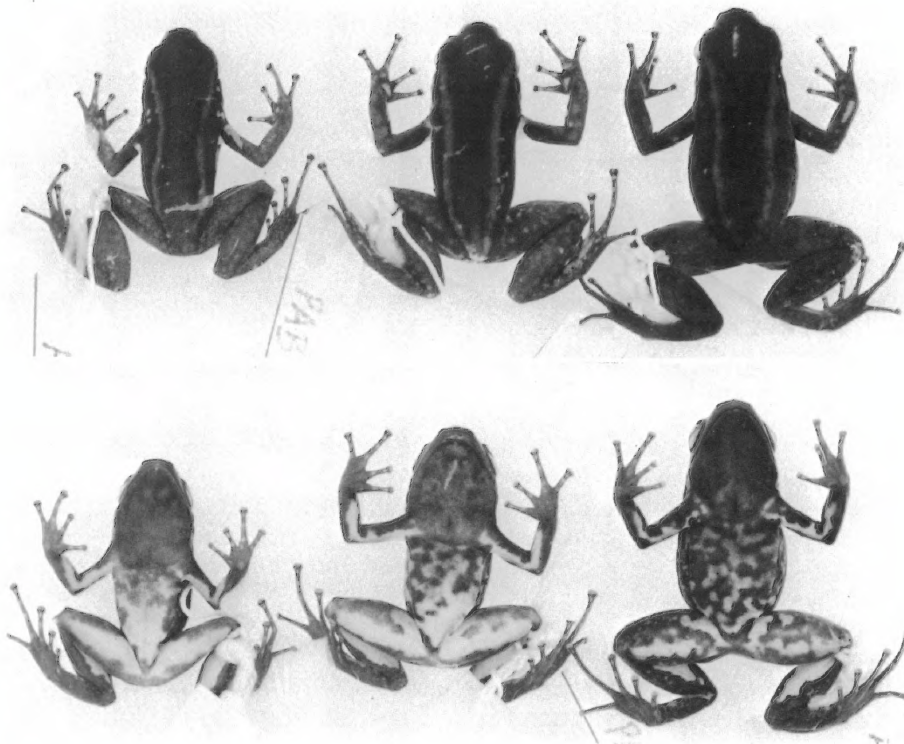


Fig. 4. Color pattern and size variation in adult *Dendrobates andinus*, new species, $\times 1.5$. Dorsal and ventral views of same specimens, left to right: IND-AN 1555 (♂), 1538 (♀), 1556 (♀ holotype).

terior portion of belly mottled dark brown with bluish green marbling; posterior part of belly variably mottled dark brown on bright yellow. The undersides of the arms and thighs are also variably mottled dark brown, with extensive areas of bright yellow. A bright yellow axillary spot is continuous with a yellow stripe on the underside of the upper arm. An elongated bright yellow marking (calf spot) extends proximoventrally from behind the knee for most of the length of the shank. The undersides of the hands and feet are brown. The iris is brown.

The color pattern is less vivid in the somewhat faded preserved specimens, which are brown to blackish brown with pale grayish and cream markings (compare figs. 1A, 4). There is no pale line in the groin.

MYOLOGY: A few pertinent muscles were examined by cutting and reflecting flaps of skin behind the tympanum and on the thigh of IND-AN 1539. The muscles of this specimen are white in preservative, without the

heavy black or gray pigmentation that characterizes some species.

There are two distinct superficial slips of the m. depressor mandibulae, both originating from the dorsal fascia and inserting together on the posterior end of the retroarticular process of the mandible. The anterior slip is more than twice as wide as the posterior and a small part of it originates superficially from the posteroventral margin of the tympanic ring; this relatively wide slip slightly overlaps the posterodorsal margin of the tympanic ring, but its bulk also keeps the skin away from the dorsal margin of the ring, explaining why both dorsal and posterodorsal margins of the tympanum are externally concealed. The narrow posterior slip dorsally overlaps the m. dorsalis scapulae. The anterior superficial slip of the m. depressor mandibulae conceals a deeper slip that originates mainly from the otic ramus of the squamosal bone, with a few fibers originating from the posterior margin of the tympanic

ring. There is no m. adductor mandibulae externus (mandibular branch of trigeminal nerve is superficial). On the thigh, the distal tendon of the deep m. semitendinosus pierces the distal end of the mm. gracilis complex prior to insertion.

OSTEOLOGY: Data were obtained from X-rays (fig. 5) of IND-AN 1538, 1555, and 1556; the pectoral girdle of IND-AN 1539 was examined by dissection.

The skull is about as wide as long. Frontoparietals long and in medial contact throughout. Sphenethmoid large, in close contact with anterior ends of frontoparietals and seemingly overlapped by nasals, which are not distinguishable in the radiographs. Ventrolateral processes of sphenethmoid distally well separated from maxillae; palatines absent. Teeth present in all specimens on maxillae and premaxillae; alary processes of premaxillae inclined anterolaterally. Mandible with a pronounced retroarticular process. Eight presacral vertebrae, with no obvious fusions; sacral diapophyses barely dilated. Pectoral girdle firmisternal, with massive coracoids in broad medial contact; clavicles straight, in contact with scapulae and nearly in contact with each other at midline,



Fig. 5. *Dendrobates andinus*, new species. Radiograph of IND-AN 1556 (♀ holotype), $\times 2.2$.

where they appear to be in broad contact with the anteromedial edges of the coracoids (intervening procoracoid cartilages, if present, narrow and inconspicuous or possibly ossified and fused with coracoids); a well developed bony omosternum; a small cartilagi-

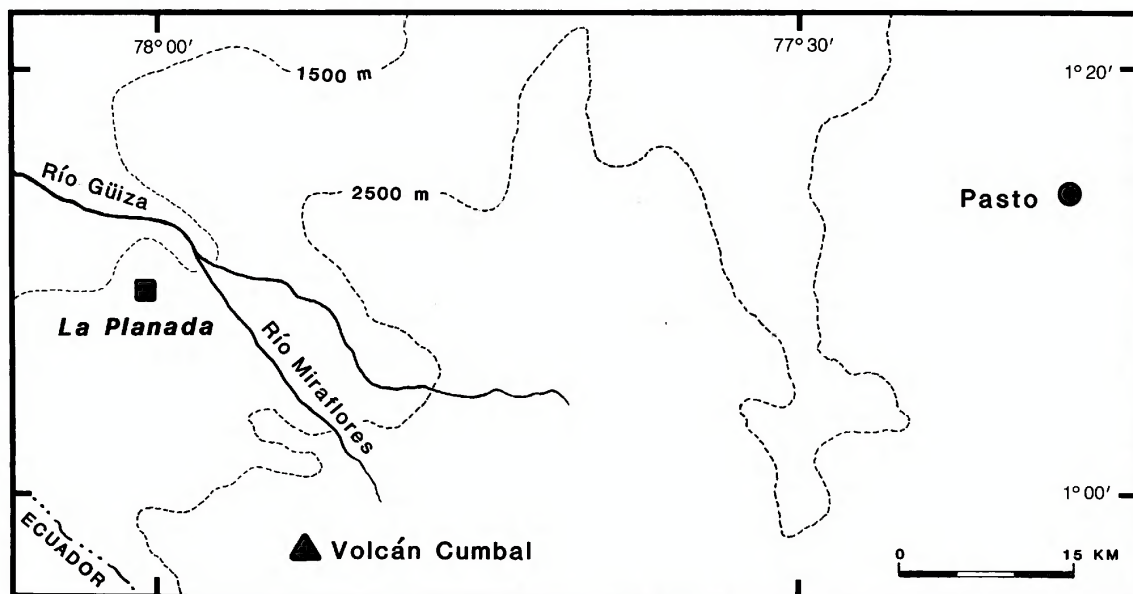


Fig. 6. Map showing location of the Reserva Natural La Planada, on Pacific drainage of Andes in extreme southwestern Colombia.



Fig. 7. View across forested plateau (~1780 m) at La Planada Reserve, type locality of *Dendrobates andinus*.

nous sternum, posteriorly narrowed and bluntly pointed. Phalangeal formula of hands 2-2-3-3, of feet 2-2-3-4-3. Every digit with a short, prominently T-shaped terminal phalanx (indistinct in fig. 5), with the transverse process lying nearly at the middle of the fleshy disc; each transverse process is relatively wide from end to end, wider than the length of its basal stem and more than two times the width of the penultimate phalanx at midpoint.

DISTRIBUTION AND NATURAL HISTORY

DISTRIBUTION AND HABITAT: *Dendrobates andinus* is known exclusively from La Planada Nature Reserve, on the Pacific versant of the Andes in extreme southwestern Colombia (fig. 6). Although specimens were collected only at an elevation of 1780 m, the species was seen and heard (see Behavior below) in an elevational range of 1700–2020 m.

The 1667-ha reserve is in montane rain forest—or in the “subtropical very humid premontane life zone” of the Holdridge clas-

sification.³ Most of La Planada is a forested plateau, as implied by its Spanish name (plano = flat). This plateau (fig. 7) is about 1780 m above sea level, but the reserve in total spans an elevational range of 1200–2100 m. The area is drained by many cold (18°C) clear-water streams that flow over rock, gravel, and sand. Most of these waterways eventually empty into the Río Güiza or Río Nulpe as part of the Río Mira drainage.

Based on weather data from 1985 and 1986 (G. Cantillo, personal commun.), the annual precipitation at La Planada is an estimated 5000 mm. During the few months that fieldwork was conducted (April–June 1986), average temperature varied from a nighttime low of 13.1°C to a noontime high of 22.8°C. A sudden temperature drop to 18°C usually occurred in midafternoon when a dense mass

³ The area is shown as “bosque muy húmedo premontano” in map 17 of *Carta Ecológica [de Colombia]*, scale 1:500,000 (in Espinal et al., 1977). See Myers (1969: 9–12) for a still-pertinent critique of the Holdridge system.



Fig. 8. Interior of the wet montane forest at La Planada Reserve, at an elevation of about 1780 m.

of low clouds covered the reserve. Measurable rain fell on all but five days in April–June 1986; rain typically commenced at about 16:00 hr and continued throughout the night, with an average daily precipitation of 15 mm. High humidity is maintained by the nearly constant cloud cover, frequent rainfall, and abundance of streams.

A portion of the forest at La Planada has

suffered slight disturbance in the past owing to clearings for pasture and trails opened for the extraction of commercial timber. Most of the forest, however, remains intact. Trees have a maximum height of 25 m and are covered by epiphytic plants, most noticeably those of the families Araceae, Bromeliaceae, and Orchidaceae. The tree canopy is dense and allows little penetration of light, thereby



Fig. 9. Clutch of three *Dendrobates andinus* eggs on bromeliad leaf.

contributing to low rates of evapotranspiration and high humidity. There is a moderate to dense understory of saplings or small trees, palms, and tree ferns, and a ground layer of herbaceous plants (fig. 8). The forest floor is permanently covered by leaf litter and fallen tree branches or trunks colonized by a diversity of fungi, mosses, and lichens.

BEHAVIOR: *Dendrobates andinus* is diurnal. Specimens were found only by examining water-filled bromeliads, either on live tree branches or on branches that had fallen to the ground. *D. andinus* has a distinctive call comprised of a series of well-spaced "crreek" notes. This call was frequently heard from various heights in trees throughout the forest in an elevational range of 1700–2020 m. Thus, the species seems to be predominantly arboreal. Although its vertical distribution in forest trees could not be determined, it possibly is more related to vertical bromeliad distribution than to height per se (as hypothesized for the Panamanian *D. arboreus* Myers et al., 1984).

Except for its distinctive call, *Dendrobates andinus* is inconspicuous in the forest. Individuals sit in the basal portions of bromeliads, where the plant is filled with debris and rainwater and its leaves are pale yellowish green. In this situation, the frog's pale-spotted limbs and yellowish dorsolateral

stripes on a blackish body seem to be more a disruptive camouflaging pattern, rather than an aposematic one (although the color pattern might well serve both functions depending on circumstances). When an individual is approached, it immediately stops calling and seeks cover deep in the bromeliad. It may also attempt to escape by quickly hopping away and hiding in another part of the bromeliad or in nearby mosses or leaf litter.

Because of frequently unsuccessful efforts to capture the frogs, several bromeliads where activity was observed were marked with red plastic tape and checked periodically. Frogs usually were seen in the marked bromeliads on subsequent days. In an attempt to determine whether the frogs have site-specific behavior, three were captured, marked (toe-clipped), and released. Within a five-day period, two of these frogs were recaptured twice at the same plant. Therefore it seems that an individual frog has some degree of site fidelity to a particular bromeliad, although defensive territorialism was not observed.

REPRODUCTION AND COURTSHIP: The egg clutch of *Dendrobates andinus* comprises three or four black eggs with relatively large jelly capsules (fig. 9). They are deposited in bromeliads above the water line. On two occasions an adult frog was found near an egg clutch but escaped before it could be captured to determine its sex; Mr. G. Cantillo found one frog with two small black tadpoles on its back. Egg attendance by a nurse frog of one sex or the other, and subsequent tadpole carrying, is believed to be universal among dendrobatids (e.g., Myers and Daly, 1983).

Courtship was observed once, on an outer leaf of a bromeliad attached to a fallen branch, about 80 cm aboveground: Activity commenced at 11:05 hr and involved three individuals—an actively calling male near the distal end of the leaf, and two other frogs (X, a probable female, and Y, a probable male) which were first seen on the basal part of the leaf. Frogs X and Y moved toward the calling male, but frog Y stopped at the edge of the leaf while frog X approached close to the male. When X was positioned directly facing the male it remained motionless for about 5 min, until the male stopped vocalizing. Then, X lowered its head, pressed its ventral surfaces against the leaf, and spread its legs away from

the body. The male subsequently moved forward, turned around, and proceeded to mount X, wrapping its forelimbs around X's head and letting its hind limbs hang loose. This embrace appears to have been typical cephalic amplexus, so named by Myers et al. (1978: 324–325) and subsequently observed in a variety of dendrobatids.

The male and frog X remained coupled for about 45 min; at 15–20-sec intervals X would rise on its legs and hop a short distance, thereby briefly changing the pair's orientation on the leaf. During this time frog Y remained on one side of the leaf a few centimeters away from the coupled pair. Then, possibly due to disturbance caused by photographic flash, the pair separated.

Shortly after the above separation, the original male and frog Y both began to call, but these calls had a lower pitch and seemingly a faster rate than the original advertisement call. From this calling match, it seemed that Y also was probably a male.⁴ The two calling frogs approached and faced one another to within a distance of less than 1 cm. Frog Y then stopped vocalizing, lowered its head, and pressed its ventral surfaces to the leaf, with spread legs, just as X had done earlier. The original, apparently dominant, male mounted Y in a cephalic embrace in the same manner as he had mounted X an hour before. They remained coupled for about 40 min, but the shaking and rotating body movements of Y were more frequent than in the earlier behavior of amplexed X. The original male and Y then separated and the dominant male resumed calling almost immediately, while Y moved back to its earlier position at the edge of the leaf and remained silent.

About 10 min later the behavioral sequence was repeated between the original male and frog X, which had remained in fairly close proximity to the male's encounter with Y. Frog X approached the calling male who again mounted it as described at the beginning of this account. Observations of this coupled pair were discontinued 30 min later,

but the site was marked with red tape. That night, a clutch of four eggs was found on the basal part of the same bromeliad leaf where courtship had been observed in late morning. An adult frog jumped from the leaf when the bromeliad was handled.

Assuming that frog Y was a contender with the dominant male as a potential mate for frog X (evidently a female as it never vocalized), the cephalic embrace used by the original male on both X and Y might be interpreted as true mating amplexus in the first case and as aggressive behavior in the second. Retention of the cephalic embrace in an aggressive context has been documented for certain dendrobatids that have lost amplexus during actual mating (Myers et al., 1978: 324–325; 1984: 14), but published details about this are scarce. Egg laying and fertilization by *D. andinus* were not observed and so the question of whether cephalic amplexus is maintained to climax remains unanswered in this species.

SYSTEMATICS

The new frog described herein belongs to the family Dendrobatidae, as shown by a suite of characters including paired digital scutes, jaw and thigh musculature, skull features such as retroarticular process of mandible, firmisternal pectoral girdle, T-shaped terminal phalanges, general habitus (Myers and Ford, 1986: 9–12), tadpole carrying, and cephalic amplexus. It specifically belongs to the *Dendrobates-Phyllobates* lineage, the monophyly of which is best defined at present by piperidine skin alkaloids (e.g., Myers and Daly, 1983; Daly et al., 1987). Such alkaloids almost certainly will be found in *Dendrobates andinus* if methanolic skin extracts become available for analysis. Meanwhile, its relationships must be sought with morphological and weak bioacoustical criteria.

Dendrobates andinus is primitive in its retention of teeth on the maxillary arch, derived in having a slightly shortened first finger, and seemingly intermediate between primitive and derived states in having only modest expansion of the finger discs. This character mixture would place it in an intermediate position between *Dendrobates* and *Phyllobates* as revised by Silverstone (1975,

⁴ We say "probably" because there is such a thing as female vocalization among frogs, including at least one species of dendrobatid. Wells (1980) described a close-range encounter call given by both male and female *Colostethus inguinalis*.



Fig. 10. *Dendrobates erythromos*, AMNH 104864 from Centro Científico Río Palenque (type locality), 170 m, Pichincha, Ecuador.

1976). But *Phyllobates* has since been reduced to a small monophyletic cluster of Central American and western Colombian species defined by presence of batrachotoxins (unique steroidal alkaloids of incredible toxicity), and the remaining species were transferred to *Dendrobates* pending completion of phylogenetic analyses of that composite genus (Myers et al., 1978). The present generic situation was concisely summarized by Maxson and Myers (1985), except that *Atopophrynus* subsequently was removed from the family (Myers and Ford, 1986).

As indicated in the Diagnosis and figure 1, the coloration of *Dendrobates andinus*, particularly the bright dorsolateral stripes, is remarkably similar to that of *D. truncatus* and especially that of *P. aurotaenia*; these species are readily separated, however, and details of hand structure (fig. 2) seem to preclude close relationship. Dorsolateral stripes do occur elsewhere in *Dendrobates*, although mainly in dwarf species of the *minutus* and *quinquevittatus* groups (Myers and Daly, 1980; Myers, 1982), none of which seems close to *D. andinus*. Both dorsolateral and oblique lateral stripes are widespread in the Dendrobatidae and it is difficult at this time to judge if one is more primitive, or if there is a high degree of homoplasy. Both kinds of stripes

may occur together, as in the recently described *D. azureiventris*.⁵ Thus, although features of color pattern do provide clues to relationships among dendrobatids, sympleiomorphy, homoplasy, and, in some groups, extraordinary radiation make color and pattern less reliable than is generally realized.

It may be that the nearest relative of *Dendrobates andinus* remains to be discovered in wet montane forest of the Ecuadorian and Colombian Andes. Unless such a species is found, however, the sister-species of the arboreal, high-elevation *D. andinus* seems to be, surprisingly, a terrestrial low-elevation species: It is *Dendrobates erythromos* (fig. 10), described on the basis of seven specimens and three tadpoles from a locality in the Pacific lowlands of Ecuador, some 200 km SW of the type locality of *D. andinus*. The following comparisons with *andinus* are based partly on the type description of *erythromos* (Vigle and Miyata, 1980) and mainly on 14 topotypic specimens (AMNH 104850–104863, including 7 adults) collected by Myers and Daly in November 1979, with associated field notes, photographs, and a tape recording.

Comparison with *Dendrobates erythromos*

COLOR AND PATTERN: *Dendrobates erythromos* ranges from dark brown through blackish brown to black in life (as does *D.*

⁵ *Dendrobates azureiventris* (Kneller and Henle, 1985), new combination, was described as a *Phyllobates* from the Río Huallaga drainage of northern Peru. In lacking basal toe webbing and in having a well developed, albeit incomplete, lateral stripe from the groin, it seems to belong in the *Dendrobates pictus* group (sensu Silverstone, 1976), but the additional presence of dorsolateral stripes readily distinguishes *azureiventris* from all other members of the *pictus* group. Species treated in the present paper (*D. andinus*, *D. erythromos*) have dorsolateral stripes but lack the well defined lateral line of *azureiventris* and other members of the *pictus* group.

This species had also been studied and was in the process of being described by Rainer Schulte, who sent a photograph to Myers several years ago (in litt., Aug. 28, 1980). The only other known collector of this rare species is Harvey Bassler, who obtained one (AMNH 42186) in December 1925, at Achinamisa, Río Huallaga, along with two other members of the *pictus* group (*D. petersi* and *D. pictus*).



Fig. 11. Dorsal and ventral color pattern in *Dendrobates erythromos* from the type locality. Photographed before preservation; notice faint dorsolateral stripes. Left, AMNH 104850♂; right, AMNH 104851♀, $\times 1.8$.

andinus), with poorly defined, bronzy brown dorsolateral stripes (figs. 10, 11) that are in the same position as the well defined yellowish stripes of *andinus*. The ventral upper arm of each species has a bright stripe that extends into the axilla; the posterodorsal part of the

upper arm additionally is bright orange in *erythromos*, and this species lacks the bright calf marking of *andinus*. Neither species has a definite oblique pale stripe in the groin, although in life some *erythromos* have the hint of a short light blue or green line in this

TABLE 2
Comparative Size and Proportions (%) of Adult *Dendrobates andinus* and Adult *D. erythromos*

Character ^a	Sex	<i>D. andinus</i> N = 2♂ + 2♀ mean (range)	<i>D. erythromos</i> N = 3♂ + 4♀ mean (range)
Snout-vent length (SVL) in mm	♂	19.8 (19.5–20.1)	21.0 (20.0–21.6)
	♀	21.1 (20.7–21.5)	23.7 (22.4–25.2)
Tibia length/SVL	♂	50.7 (49.7–51.7)	51.5 (49.5–53.5)
	♀	51.7 (51.2–52.2)	49.4 (48.0–52.2)
Greatest head width/SVL	♂	34.6 (34.4–34.8)	36.8 (36.0–37.5)
	♀	35.8 (34.9–36.7)	36.2 (35.3–36.8)
Center naris-edge eye/eye length	♂	0.59 (0.53–0.65)	0.62 (0.61–0.63)
	♀	0.59 (0.58–0.60)	0.60 (0.56–0.65)
Hand length/SVL	♂	29.3 (28.7–29.9)	29.3 (27.6–31.0)
	♀	30.3 (30.2–30.4)	28.2 (27.3–28.7)
Hand length/head width	♂	84.7 (83.6–85.7)	79.4 (76.6–83.8)
	♀	84.8 (82.9–86.7)	77.9 (74.2–79.8)
Width 3rd finger disc/finger	♂	1.60 (1.60–1.60)	1.78 (1.60–1.75)
	♀	1.60 (N = 1)	1.70 (1.60–1.80)

^a See table 1 notes for methods of taking certain measurements.

region. Ventral surfaces of both are variably mottled brown or black, on light blue in *erythromos*, on bluish green and yellow in *andinus*; the latter has a black throat as does one specimen (male) of *erythromos*, which otherwise has the throat patterned like the belly. *D. erythromos* differs from *andinus* in having the hind limbs banded in black and brown rather than pale-spotted.

MORPHOLOGY: *Dendrobates erythromos* is a few millimeters larger than *D. andinus* (table 2). General habitus is quite similar: Each has a very short snout and a loreal region that slopes slightly outward to the lip; the tympanum is concealed dorsally as well as having the posterodorsal concealment found in dendrobatids generally. Both species have essentially smooth skin in preservative (transparencies show that, in life, *erythromos* has granular skin on the dorsum and hind limbs). Proportions are generally similar with a notable exception that *andinus* has a larger hand relative to head width and, less definitely, relative to body size; part of the hand/head difference, however, seems due to the slightly narrower head of *andinus* (table 2), although samples obviously are too small for exact analysis. The hand and foot illustration for *andinus* (fig. 3) could almost serve for *eryth-*

romos, except that the latter usually has a slightly longer first finger; the appressed first finger is slightly shorter than the second in *andinus* but in only one of seven adult *erythromos*—the first two fingers being essentially equal in the remaining six *erythromos* (“2 > 1” in the type description). Hand and foot tubercles are nearly identical and basal toe webbing is absent. Freshly skinned *erythromos* have gray flesh, but muscle pigmentation is lacking in a preserved specimen of *andinus* (see Myology). Both species have teeth on the maxillary arch.

TADPOLE: Unavailable for *D. andinus*. Vigle and Miyata (1980) gave a description for *D. erythromos*, which seems to have a rather generalized dendrobatid larva.

SKIN ALKALOIDS: Unknown in *D. andinus*, although presumably present. *D. erythromos* is capable of producing a copious white secretion that contains relatively small amounts (<50 µg/100 mg of skin) of three alkaloids (Daly et al., 1987, table 5): Alkaloids 251B of the indolizidine class and 267A of the pumiliotoxin-A class (allopumiliotoxin subclass) are the major constituents, whereas 281D, an unclassified piperidine-based alkaloid, occurs only as a trace compound. These three alkaloids in total occur in a wide

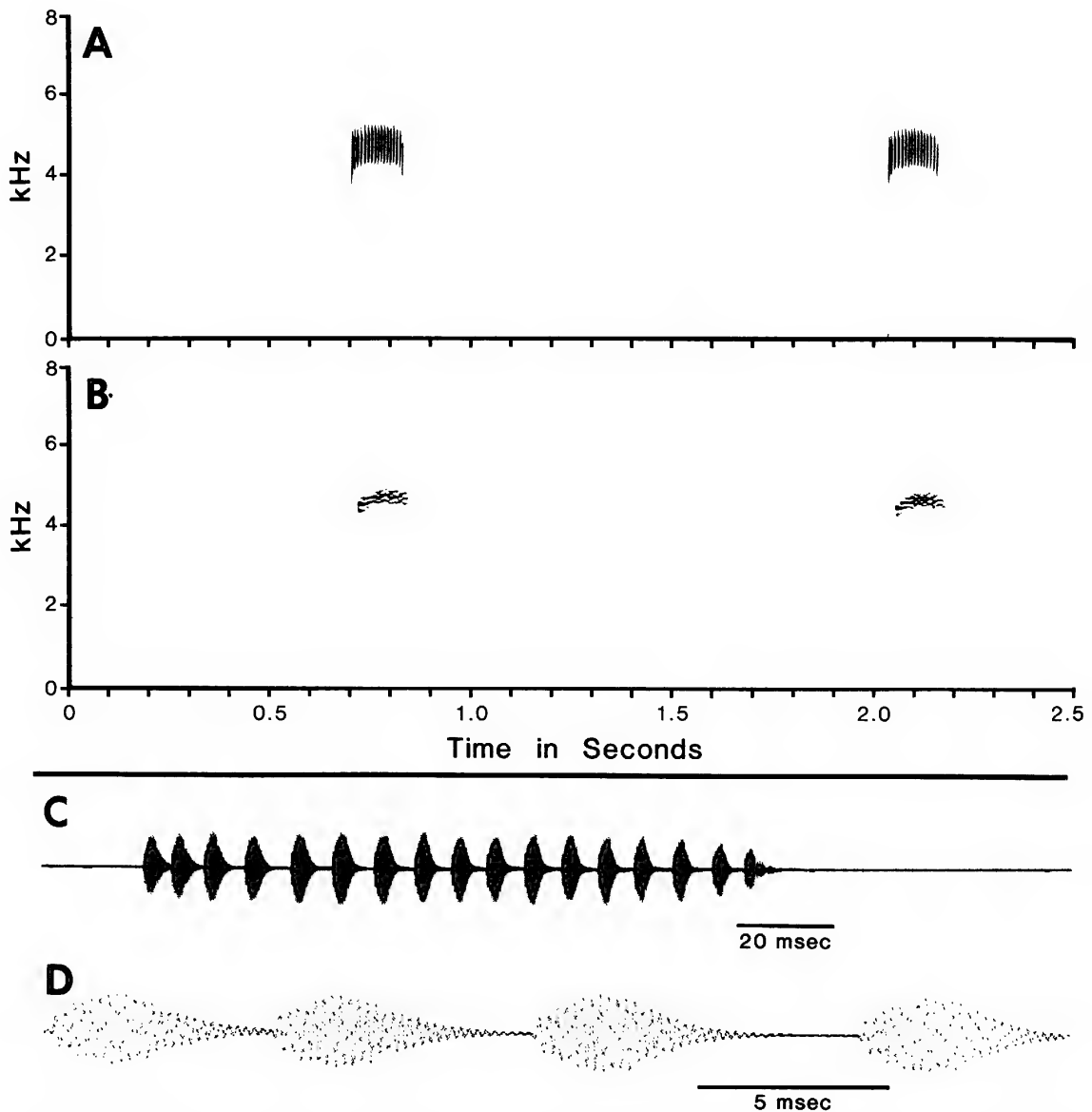


Fig. 12. Advertisement call (retarded chirp call) of *Dendrobates erythromos*: A. Wide-band (500-Hz filter) sound spectrogram showing two notes from middle of 3.6-min sequence (mean rate = 0.63 notes/sec). B. Same notes graphed with narrow-band (45 Hz) filter. C. Waveform of first note, showing strong pulsatile nature (also evident in A). D. Fine temporal structure of first four pulses in waveform above.

Specimen (AMNH 104850) recorded at Centro Científico Río Palenque, 170 m, Pichincha, Ecuador, at 9:30 a.m. on November 12, 1979; air temperature 22.0°C at calling site, a few centimeters inside hole on slope 8 m above small stream (AMNH reel 215:1).

variety of *Dendrobates* (s.l.) but are not among the small number of nonbatrachotoxin alkaloids so far detected in *Phylllobates* (s.s.) fide Daly et al. (1987, tables 3–5).

HABITS: *Dendrobates andinus* seems to be

primarily arboreal in montane rain forest. In contrast, *D. erythromos* is terrestrial in lowland rain forest. Both are wary and rather difficult to approach. Vigle and Miyata (1980: 5–6) described the habitat in which Vigle

found the first seven *erythromos* on the ground near streams. Myers and Daly (unpubl.) found that *erythromos* is rather common and widespread near small forest streams at the type locality, but that it shows a preference for lurking in dark crevices under large logs or rocks and in holes near stream banks or on the sides of ravines. This diurnal frog is best hunted by day with a flashlight!

VOCALIZATION: The advertisement call of *Dendrobates andinus* is described herein as a series of well-spaced "creek" notes. The call of *D. erythromos* is a series of well-spaced "soft repetitive chirps" (Vigle and Miyata, 1980: 6). The following analysis of the call of *erythromos* should be useful for comparison when a recording becomes available for *andinus*.⁶

Several individuals were located calling from entrances to crevices or holes (see above) near a stream-side seepage area on the morning of November 12. There was a definite tendency for all to be calling at once and for all to be silent for varying periods; disturbing one seemed to silence them all. The advertisement call is a long train of harsh but not very loud "chirps," given continuously for many seconds. The one recording made includes an unbroken sequence of 136 notes given in 3 min, 35 sec, for an overall repetition rate of 0.63 notes/sec. Spacing between notes varied from 1 to 4 sec, with an internote interval of about 1.2–1.4 sec being most typical.

Individual notes are 0.13–0.14 sec duration and have a median frequency of about 4.5 kHz. Frequency is modulated within the note, there being a slow rise and more rapid fall, as indicated by the frequency–time curvature on spectrograms (fig. 12); sections of a few notes show the dominant frequency starting at about 4300 Hz, rising to about 4700 Hz, then dropping back below 4500 Hz. The individual note is strongly pulsed at a

rate of 131 pulses/sec; the first several pulses are produced more rapidly than subsequent ones.

The individual notes uttered by *D. erythromos* are spectrographically similar to those in the synapomorphic "chirp call" of the *Dendrobates histrionicus* group (sensu Myers et al., 1984), with a few notable differences. The call of *erythromos* is produced at a slower rate (<1 note/sec) than in those of the *histrionicus* group (2–10 notes/sec). Frequency modulation is greater in the note of *erythromos*, which shows both a definite rise and fall. Pulses are produced more rapidly at the start of the *erythromos* note than in the middle or end, but pulsation starts slowly and ends rapidly in the *histrionicus* group (e.g., see figs. 9, 10 in Myers et al., 1984). Further comparisons will be desirable and conceivably might obscure some of these apparent differences. Meanwhile, the term *retarded chirp call* is proposed to differentiate the call of *D. erythromos* from the characteristic *chirp call* of the eight species of the *histrionicus* group.

CONCLUSIONS

A few similarities in the color patterns of *Dendrobates andinus* and *D. erythromos* seem correlated with an overall morphological similarity, all of which is suggestive of close (sister-species) relationship even though we cannot tell how much of this similarity might simply be plesiomorphy. Vigle and Miyata (1980) postulated that *erythromos* is a member of the *pictus* group as defined by Silverstone (1976: 35) and that it is most closely allied with *D. ingeri*, a poorly known frog from the eastern base of the Andes of southwestern Colombia (Amazonian drainage, Depto. Caquetá; see Silverstone, 1976). *Dendrobates ingeri* differs in lacking stripes and in having strongly granular skin in preservative, but it has a light axillary spot as in *andinus* and *erythromos*, and a large pale calf spot as in *andinus* (although such markings are not limited to these species). We cannot probe matters further at this time and are content to place *D. andinus* tentatively in Silverstone's *pictus* group, where *erythromos* already resides, although that loose and possibly artificial group is now diluted by the addition of species with dorsolateral stripes

⁶ A partial call of *D. erythromos*, comprising a 3.6-min sequence, was monitored on the video screen of a real-time spectrograph (Kay 7850) and recorded on light-sensitive paper with a Honeywell LS-8 fiber optic printer run at 10 mm/sec. The resulting strip chart was used for obtaining temporal data on note repetition etc. Standard spectrograms, sections (not shown), and waveforms (fig. 12) were produced with a Kay model 7800 digital spectrograph.

(i.e., *andinus*, *erythromos*, and *azureiventris* [see fn. 5]). Some frogs in the *pictus* group have a peeping or whistling sort of call quite different from the well-spaced, harsh notes of *erythromos* and also seemingly different from the enigmatic notes of *andinus*. After tape recordings are obtained for *andinus*, *ingeri*, and other species, bioacoustical analysis may help to elucidate relationships in this confusing assemblage.

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NOTE ADDED IN PROOF

C. W. Myers

The present paper was preceded unexpectedly by the following: C. W. Myers, 1987 (Sept. 5), "New generic names for some Neotropical poison frogs (Dendrobatidae)," *Papéis Avulsos Zool.*, São Paulo, 36(25):301–306.

In that publication, *Dendrobates andinus* is listed under the new genus *Epipedobates* as "*Dendrobates* n. sp., Myers and Burrowes (1987, in press)." Its name therefore becomes *Epipedobates andinus* (Myers and Burrowes), new combination.

Other species discussed in the present paper that were referred to *Epipedobates* are *E. azureiventris*, *E. erythromos*, and *E. ingeri*. The current placement of *andinus*, *erythromos*, and *azureiventris* in Silverstone's (1976) *pictus* species group (transferred in its entirety to *Epipedobates*) remains tentative, to avoid setting up new groups at this time.

Under the new arrangement, the monophyletic lineage of dendrobatids that produce piperidine and other lipophilic alkaloids is partitioned among four genera, with *Epipedobates* standing as the plesiomorphic sister-group to *Minyobates*, *Phyllobates*, and *Dendrobates*. So far as is known, the species of *Epipedobates* are nearly all terrestrial or only weakly scansorial in low vegetation. *Epipedobates andinus* consequently stands out by virtue of its arboreal habits, although its presumed sister-species (*E. erythromos*) seems entirely terrestrial.

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